

TEMPORAL DISTRIBUTION OF HATCHING TIMES IN THREE
SYMPATRIC MANTIDS (MANTODEA: MANTIDAE) WITH
IMPLICATIONS FOR NICHE SEPARATION AND COEXISTENCE

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Abstract.—Mantids are members of a guild of generalist predators in arthropod communities. Three species commonly coexist in old fields: *Tenodera sinensis* Saussure, *T. angustipennis* Saussure, and *Mantis religiosa* Linnaeus. Egg hatch occurs early in the spring, producing high predator density when prey are in short supply. First instar nymphs of the two *Tenodera* species, which are most similar in size and occupy the same vegetational stratum in the field, are most divergent in timing of egg hatch. Nymphs of *T. sinensis* hatch first, and enter the second instar as *T. angustipennis* are beginning to hatch. The timing of egg hatch for *Mantis religiosa*, which is much smaller than the other two and occupies a different portion of the vegetation, is intermediate. Therefore nymphs of the three species are not the same body size at the same time; body size determines size of prey which can be captured most efficiently. We suggest that the temporal disparity in egg hatch may be one mechanism for coexistence among these species by reducing niche overlap when resources are critically limiting.

Key Words: Mantodea, Mantidae, *Tenodera*, *Mantis*, bitrophic niche, predators, sympatry

Praying mantids (Mantodea: Mantidae) are members of a guild (*sensu* Root 1967) of generalist predators which inhabit arthropod communities. This guild includes other taxa, notably spiders, and all members have in common a bitrophic niche; they occupy both the third and fourth trophic levels by virtue of feeding on other predators as well as on herbivores. Thus, the relationship among guild members is complicated by the potential for both interspecific competition and mutual predation. Added to this is the propensity for cannibalism in some groups. Therefore, interspecific coexistence in this guild, especially among very similar species, may depend upon factors which mitigate a variety of antagonistic interactions.

Three similar species of mantids com-

monly co-occur in northern Delaware. *Tenodera sinensis* Saussure, the largest of the three, was originally introduced from the orient near Philadelphia, Pennsylvania, in 1896 (Laurent 1898), and has occurred in Delaware at least since the 1930s (Jones 1933). Its congener, *T. angustipennis* Saussure, was found in Maryland in 1926 (Gurney 1950), and had become established in Delaware by 1930 (Jones 1933). *Mantis religiosa* Linnaeus, the smallest of the three, was introduced into the northeastern United States in 1899 (Gurney 1950); its duration of residence in Delaware is uncertain (Rathet and Hurd 1983). All three species are sympatric in Asia (Jing-jin et al. 1981).

We have been studying various populations of mantids, especially *T. sinensis*, in

northern Delaware over the past decade (Eisenberg and Hurd 1977, Hurd et al. 1978, Eisenberg et al. 1981, Rathet and Hurd 1983, Hurd and Eisenberg 1984a, b, Hurd 1985, Hurd and Rathet 1986, Hurd 1988). We have observed that all three species can be found in the same general habitat: successional old fields. Emergence from oothecae takes place in early spring when arthropod biomass is very low. In fact, mantid biomass at egg hatch is apt to be much greater than biomass of all other arthropods combined, so nymphs are likely to be severely food limited (Hurd and Eisenberg 1984a, b). It is therefore reasonable to ask: how do the niches of these similar predators differ to allow them to coexist in a limited environment? Rathet and Hurd (1983) found that both *Tenodera* species occupy the same vegetational stratum (30–60 cm foliage height), whereas *M. religiosa* is generally found lower in the vegetation (5–25 cm). Therefore, *M. religiosa* may escape predation from the two larger species, although this does not rule out interspecific competition. Rathet and Hurd (1983) also found that appearance of first instar nymphs in the field was not simultaneous among the three species, and that as a consequence there was a consistent interspecific size difference throughout the season. Mantid nymphs of different sizes have different optimal prey sizes based upon capture efficiency (Bartley 1983). In the present study we ask whether there is an intrinsic difference in timing of egg hatch which could be another mechanism which reduces niche overlap in this guild of generalist predators.

MATERIALS AND METHODS

We collected oothecae of *T. sinensis*, *T. angustipennis*, and *M. religiosa* from two old fields in Newark, New Castle County, Delaware, on 10 February 1986. The collection sites are approximately 3 km apart, and represent somewhat different vegetational assemblages. One field is located on the experimental farm property of the School

of Agriculture, University of Delaware (= site AG), and dominated by a dense ground cover of timothy (*Phleum pratense*) and blue-stemmed grass (*Poa compressa*) with patches of goldenrod (*Solidago* spp.) and thistle (*Cirsium canadensis*). The other site is adjacent to the Chrysler plant in Newark (= site CHRY), and is dominated by goldenrod with a sparse ground cover of grasses, chiefly timothy.

Twelve oothecae of each mantid species from each of the two field sites were returned to the laboratory and immediately placed in separate containers and incubated at 25°C and ambient light. When eggs hatched, newly emerged nymphs were removed from the containers and killed by freezing, after which they were counted. A random sample of 20–30 nymphs from each group was measured for body length (tip of abdomen to front of head).

RESULTS

Tenodera sinensis began hatching after 18 days of incubation, and hatching continued for 11 days from oothecae collected from both sites, with a few nymphs emerging from AG oothecae as late as day 33 (Fig. 1). The pattern of hatching was sporadic with no clear difference between field sites. In only two cases did nymphs emerge on two or more consecutive days from the same ootheca, which is consistent with results from Eisenberg and Hurd (1977). Mean size of nymphs from site CHRY (9.7 mm, SD = 0.37) was somewhat larger than from site AG (9.4 mm, SD = 0.40) ($t = -2.84$, $df = 48$, $P < 0.01$).

Tenodera angustipennis did not start hatching until *T. sinensis* had finished, and duration of hatch was six days (Fig. 1). The pattern of hatching was nearly identical for eggs from both sites. Only one ootheca exhibited hatching on two consecutive days. Mean body length of nymphs (8.9 mm, SD = 0.20) was not different between sites.

Mantis religiosa was the only one of the three species to exhibit a marked site dif-

ference in hatching pattern (Fig. 1). Hatching time was intermediate, and overlapped with both *Tenodera* species. Unlike *Tenodera* spp., all but one ootheca produced nymphs on consecutive days, as many as five days in a row. As with *T. sinensis*, nymphs from site CHRY were larger (6.1 mm, SD = 0.31) than nymphs from site AG (mean = 5.8 mm, SD = 0.20) ($t = -3.78$, $df = 58$, $P < 0.001$).

DISCUSSION

We found that under identical laboratory conditions of a "common garden" experiment, eggs of *T. sinensis* hatch before those of the other two species. This is in agreement with field observations of first appearance of nymphs (Rathet and Hurd 1983), and indicates an intrinsic difference between species. Matura (pers. comm.) has also observed that *T. sinensis* hatches before *T. angustipennis* in Japanese fields.

A potential significance of this phenological difference is a reduction in overlap among species with regard to optimal prey size (Bartley 1983), which could reduce competition for limited food early in the growing season: by the time *T. angustipennis* and *M. religiosa* begin to hatch, the earliest *T. sinensis* nymphs would be entering the second instar (Hurd and Eisenberg 1984a, Hurd and Rathet 1986). This is likely to be more important for the two *Tenodera* species, since they are similar in size at emergence and occupy the same vegetational stratum, than for *M. religiosa* which occupies a different portion of the vegetation (Rathet and Hurd 1983) and is much smaller. The fact that the timing of egg hatch in *M. religiosa* overlaps the other two species may be further indication that interaction between these genera is less important than between species of *Tenodera*. Of course the question remains as to whether the temporal differences in hatching arose from historic interspecific competition, or represent a fortuitous preadaptation to living in the same habitat.

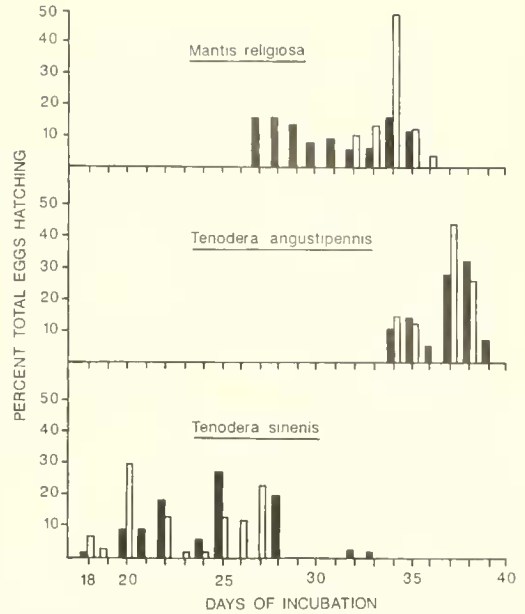


Fig. 1. Timing and pattern of egg hatch, as a percent of total eggs hatching for each species from oothecae collected at two field sites: AG = shaded bars, CHRY = open bars.

In instances where food is severely limiting, the size difference between second instar nymphs of *T. sinensis* and first instar *T. angustipennis* would confer an additional benefit on the former species, that of being able to use its congener (and later-hatching conspecifics) as a food source. We have observed in the laboratory that intra-instar predation between and within these congeneric nymphs is relatively uncommon, as is the case with *M. religiosa* according to Roeder (1936). However, we have also observed that the difference in size between successive instars is sufficiently great to provoke much cannibalism and interspecific predation (Hurd 1988). This may help to explain why we have never found *T. angustipennis* to be abundant in fields wherein *T. sinensis* was well-established.

We found two indications of differences between field sites: the difference in hatching patterns for *M. religiosa*, and the larger nymphs at site CHRY for both this species and *T. sinensis*. The difference in nymph

size may well be an indication of differences in feeding conditions for adult mantids during the previous season. Eisenberg et al. (1981) found that food limitation among adults plays an important role in biomass of oothecae; egg size may also be affected. This would indicate that adults of these two species were more food limited at site AG than at site CHRY. We are currently testing this.

Another possibility is that the size differences represent ecotypes for one or both species. This remains to be tested, as does the question of what is the gain in fitness by hatching at a larger size? One possibility is a decline in time of development, although *T. sinensis*, at least, is flexible in this regard (Hurd and Rathet 1986). We cannot as yet offer a satisfactory explanation for the difference in hatching patterns for *M. religiosa* (unless ecotypic); however, roughly the same pattern difference was observed the following year (unpublished data). The question of the significance of multiple consecutive-day hatching of eggs in this species also remains to be answered.

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